

Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity

(perceptual learning/preattentive vision/orientation gradient/monocularity)

AVI KARNI^{*†} AND DOV SAGI^{*}

^{*}Department of Applied Mathematics and Computer Science, Weizmann Institute of Science, Rehovot 76100, Israel; and [†]Department of Neurology, Chaim Sheba Medical Center, Tel-Hashomer 52621, Israel

Communicated by Bela Julesz, January 28, 1991 (received for review October 16, 1990)

ABSTRACT In terms of functional anatomy, where does learning occur when, for a basic visual discrimination task, performance improves with practice (perceptual learning)? We report remarkable long-term learning in a simple texture discrimination task where learning is specific for retinal input. This learning is (i) local (in a retinotopic sense), (ii) orientation specific but asymmetric (it is specific for background but not for target-element orientation), and (iii) strongly monocular (there is little interocular transfer of learning). Our results suggest that learning involves experience-dependent changes at a level of the visual system where monocularity and the retinotopic organization of the visual input are still retained and where different orientations are processed separately. These results can be interpreted in terms of local plasticity induced by retinal input in early visual processing in human adults, presumably at the level of orientation-gradient sensitive cells in primary visual cortex.

Early visual processing is believed to be “hard-wired” in adult mammals. Yet for some simple visual discrimination tasks, performance improves with practice—i.e., a genuine increase in sensitivity is induced by sensory experience (perceptual learning). Some instances of perceptual learning are specific for particular stimulus parameters and do not transfer when these are changed (1–4). This has interesting implications for understanding sensory processing because the dependence of learning on specific stimulus parameters could provide an effective probe to the functional architecture of the sensory system. We applied this logic to investigate the effects of training on simple texture discrimination and explored the possibility that strictly local, orientation-sensitive mechanisms were selectively involved in the learning process.

We were motivated by the observation that although recent theories of vision suggest that some texture segregations are accomplished very early in visual processing in an “automatic” (preattentive) way [i.e., without the need for higher level (attentive) recognition (5–8)], observers improve with practice even in simple, preattentive texture discrimination. Previous work referred to the “overlearning” of the limitations of “nonautomatic” attentive vision or difficult texture discriminations (6, 9). We were intrigued by the fact that observers seemed to improve even in simple automatic texture segregation. If learning is indeed local and orientation specific, it must presumably involve changes at an early, low-level processing stage where the retinotopic organization of visual input is retained and different orientations are handled separately (10, 11). A high degree of monocularity (i.e., learning that would not transfer from a trained to an untrained eye) would suggest that learning affected a level

within the visual system where cells preferentially respond to input from one retina (monocular cells) (10, 11).

METHODS

One of the authors (A.K.) and five naive observers participated in the experiments. Experimental sessions were spaced 1–2 days apart and were carried out in an isolated dark environment. Each session consisted of 16–20 blocks of trials with 50 trials (stimulus presentations) in each block, constituting presentation of about 1000 stimuli per session. The stimuli were computer-generated textures, with a target (foreground) made of three line elements differing only in orientation from a background of horizontal elements (Fig. 1 *Left*). The only variable used in defining the target was the orientation of foreground and background elements because of extensive evidence (i) that oriented bars constitute a prime dimension of early visual cortical analysis (10, 11) and, in particular, (ii) that element orientation differences give rise to a strong preattentive perception of texture segregation (8, 12). The exact position of the target was varied randomly from trial to trial but always within a restricted stimulus area (quadrant or hemifield), thus enabling measurement of learning transfer between different regions of the visual field. Fixation was enforced by a concurrent forced-choice letter-discrimination task, between a T and an L, at the center of each display (Fig. 1 *Left*). We verified that performance on the letter-discrimination task was comparable to reference (control) performance with the same task carried out alone. Incremental performance would indicate nonoptimal fixation because performance in this task is critically dependent on eccentricity (13). Since stimuli were exposed for only a short duration (10 ms), no eye movement could displace the stimulus on the retina. This ensured that for each observer the target texture consistently appeared in a specific quadrant of the visual field.

For each display, observers were asked first to identify the letter at fixation point and then to decide whether the foreground texture was vertical or horizontal. Note that the task did not involve the discrimination of target-element orientations, which were fixed at 45° or 135° throughout the training period, but rather the orientation of the target configuration defined by the three target elements.

Observers were instructed to fixate a small central cross and then activate the trial sequence: blank screen interval (250–300 ms), the stimulus (10 ms), blank interstimulus interval, the mask (100 ms), and blank screen until response (no time limit). Immediate auditory feedback was given only for the fixation control task. Performance was measured as the mean percent correct response for different time intervals between stimulus and mask (stimulus-to-mask-onset asynchrony, SOA). As the SOA sets the temporal limit of stimulus availability (including visual persistence), it is a measure of

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviation: SOA, stimulus-to-mask-onset asynchrony.

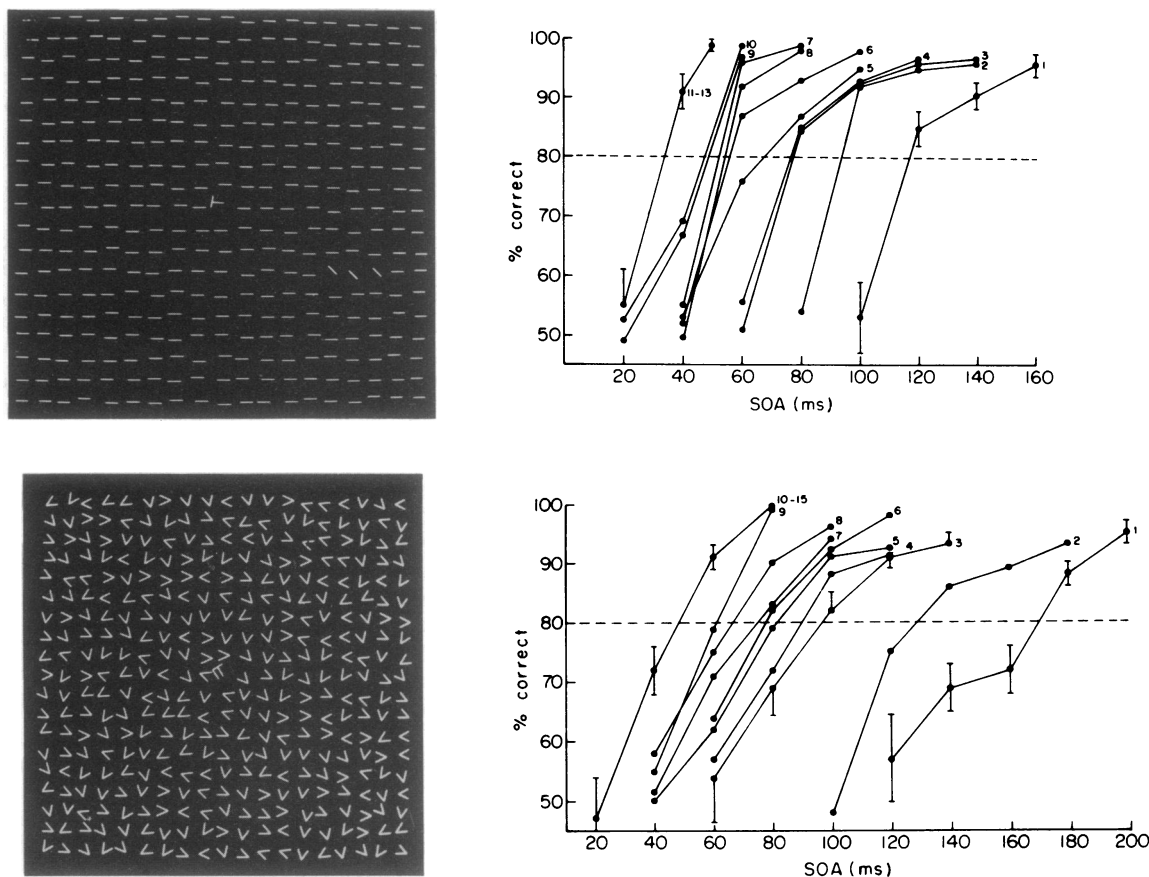


FIG. 1. Computer generated displays (Left). (Upper Left) A small target texture (three diagonal bars) embedded within a background of horizontal bars. Display size was 14° by 14° of visual angle viewed from a distance of 110 cm. The display was composed of green line segments ($0.42^\circ \times 0.03^\circ$ each of luminance 35 cd/m^2 spaced 0.70° apart) "jittered" on a black background within a 19×19 lattice. Target position was varied randomly from trial to trial but always within a specific display quadrant and within 2.5° – 5° visual angle from center of display. (Lower Left) Mask pattern made of randomly oriented V-shaped micropatterns and a central compound pattern of superimposed T and L. Psychometric curves (Right). Subjects: S.W. (Upper Right) and S.T. (Lower Right). Curves depict the mean percent correct performance for texture target discrimination on consecutive sessions (spaced 1–2 days apart). Each data point represents the mean percent correct responses \pm SD from three to five blocks (150–250 trials) for a specific stimulus-to-mask-onset asynchrony (SOA). The initial performance curve is on the right; as learning occurs, the curves are displaced to the left (shorter SOA needed for task performance). The left-most curve represents asymptotic performance. Note that curve shape (slope) for a specific observer does not change, indicating a genuine change in sensitivity. ---, 80% correct (threshold) performance.

the time observers need to obtain a workable percept (representation) of the stimulus (8, 14).

In the first session for each observer, the SOA for 95% correct responses in the texture discrimination task was determined by setting the SOA to 240–300 ms. Then on each session thereafter, 150–250 consecutive trials were run per SOA and a psychometric curve was constructed giving the correct response rate as a function of SOA. The SOA was set at the beginning of each session to the lowest SOA in which a 95% correct performance was obtained in the previous session and then was decreased in steps of 20 ms to chance performance. To evaluate changes in texture-discrimination performance with training, the SOA required by the subject to reach 80% correct responses (threshold SOA) was interpolated from the psychometric curves for each session (Fig. 1 Right).

RESULTS

The results for five observers are presented in Fig. 2, where learning curves depict the SOA for 80% correct discrimination for consecutive sessions. The required SOA was more than halved with practice. The median threshold SOA for the first session was 132 ms (range 112–170 ms) and fell to an

asymptote of 48 ms (median, range 32–58 ms) for the five observers.

Learning is rapid at first and then slows down, and a steady level of performance is achieved after 5–10 consecutive sessions. Note that the increments in performance are long-term and refer to learning retained from one daily session to the next. We found no immediate learning effects—i.e., when the first and last blocks of trials were compared for each SOA within a session. This is quite a different time scale from previously reported perceptual learning paradigms (1–3). Experiments to be reported in detail elsewhere have shown that learning is not effective in the first hour after the training session but is apparent 6 hours later and is completely retained 5 weeks later.

This improvement was not transferrable to the contralateral hemifield nor to the untrained quadrant on the trained side. Fig. 2 depicts the threshold SOA for an identical texture-discrimination task but with the target texture projected to an untrained quadrant of the display. The median threshold SOA for the five observers that took part in this experiment was 110 ms (range 100–135 ms) as compared with 48 ms (range 32–58 ms) for the preceding session for the trained visual quadrant. Thus, when the same visual task was presented to a new visual field locality, even one subserved by the same hemisphere and removed by just 3° of visual

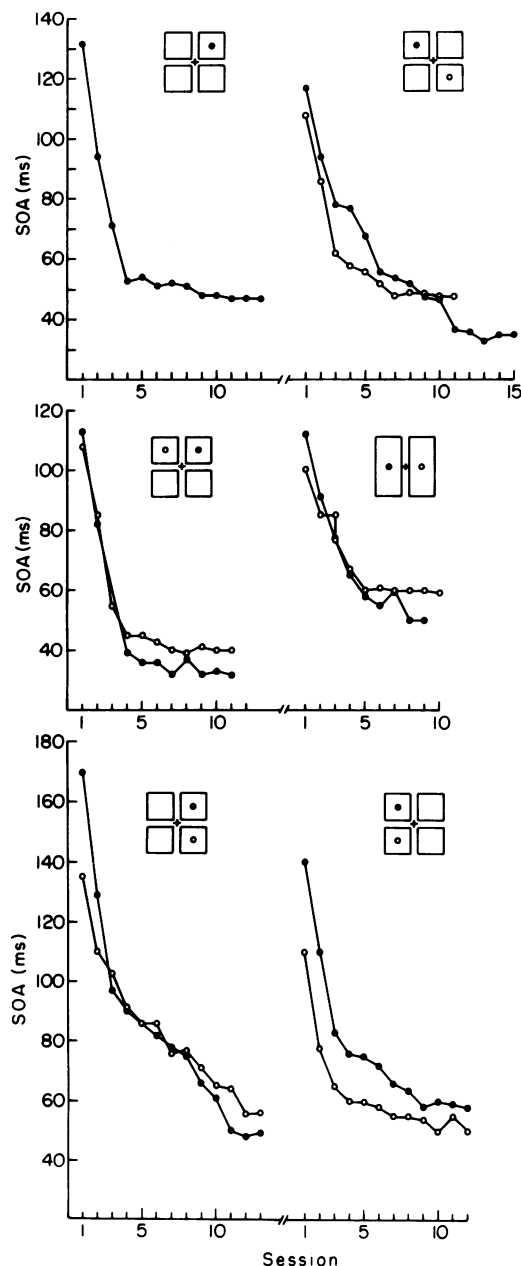


FIG. 2. Learning curves. SOA required for threshold discrimination on consecutive sessions. Each point refers to a single session, interpolated from the respective psychometric curve. The learning curves for two locations are superimposed: ●, first trained location; ○, second trained location. (Insets) Display quadrants in which target texture was presented. (Top Left and Right) Observer S.W.: target texture in right upper quadrant (Left) (●), in left upper quadrant (Right) (○), and in right lower quadrant (Right) (○). (Middle Left) Observer H.L.: target presented to right upper quadrant (●) and moved to left upper quadrant (○). (Middle Right) Observer Y.L.: target in left hemifield (●) and moved to right hemifield (○). (Bottom Left) Observer S.T.: target in upper right quadrant (●) and in lower right quadrant (○). (Bottom right) Observer A.K.: target in upper left quadrant (●) and moved to left lower quadrant (○). Observer H.L. trained with background elements set in vertical orientation throughout.

angle (at an approximate eccentricity of 4°) from a previously trained locality, the task had to be relearned. It again took observers 5–10 daily sessions to relearn the task, and when relearning for the new locality was established, the asymptotic performance level was comparable to the level attained for the initial series (Fig. 2).

Once asymptotic performance was reached for a specific locality, we investigated the specificity of the learning process for the main stimulus feature (i.e., the orientation of the texture elements) by several one-step changes. These changes were unknown to the four naive observers. The first change—to an orthogonal orientation of the target elements (from left oblique to right oblique or vice versa)—produced no significant change from the asymptotic value (Fig. 3). Next, target element orientation was set to vertical, while leaving all other display parameters as in the initial series. This had the effect of increasing the absolute gradient between foreground and background elements from 45° to 90° . As can be seen from Fig. 3, performance was better than the asymptote for this condition, yet returned to the asymptote in the following control session with the original trained orientations. However, the third change, which introduced the orthogonal orientation for the background elements while maintaining the practiced target element orientation, produced a dramatic decrease in performance (Fig. 3). The threshold SOA was 110 ms (median, range 93–118 ms), which is significantly higher than the threshold for preceding asymptotic trials and above that for a control session with the original background element orientation. Though exposed to the display for more than 10,000 times during these experiments, none of our four naive subjects could name the specific orientation of the target or background elements.

We next investigated the interocular transfer of learning. Using the same visual stimulus, three observers trained with one eye only, the other eye being covered with an opaque patch. The rate and magnitude of learning were comparable to binocular training. For a trained visual field locality, the threshold SOA for discrimination decreased from 113 ms (median, range 111–126 ms) to 49 ms (range 36–55 ms), reaching the asymptotic value after 5–10 sessions (Fig. 4). Yet when the same task was presented monocularly to the untrained eye, the required SOA was 104 ms (median, range 92–108 ms), a mean of 18% transfer between the two eyes. This is comparable to the improvement in performance

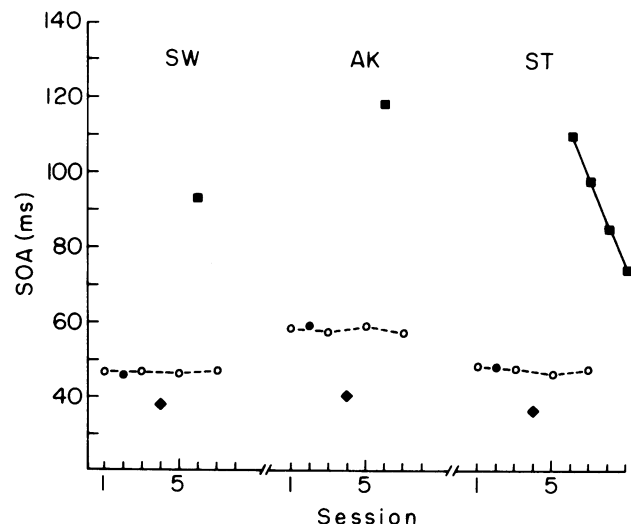


FIG. 3. The effects of element orientation changes. Threshold SOA for control learned orientations (○) and for the one-step orientation-change sessions for observers S.W. (Left), A.K. (Middle), and S.T. (Right). ●, Target element set in orthogonal orientation; ◆, target element set vertically; ■, background elements set in orthogonal orientation to control. Learning is specific for background but not target-element orientation. Performance level seems to be dependent on the absolute gradient between target-element orientation and background-element orientation, even after maximal learning. Sessions 6–9 for observer S.T. depict new learning for the orthogonal background-element orientation.

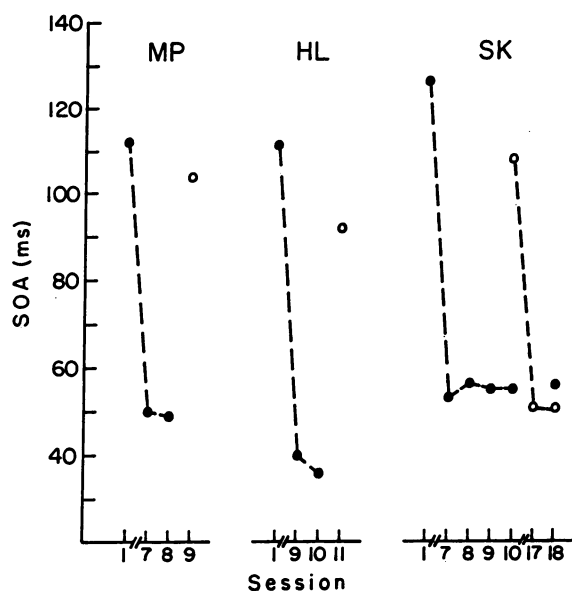


FIG. 4. Monocular learning. Threshold SOA for monocular texture discrimination for observers M.P. (Left), H.L. (Middle), and S.K. (Right). ●, First eye; ○, second eye. For each observer, prelearning and asymptotic (postlearning) performance is shown connected by the dashed lines. Sessions 10–17 for observer S.K. depict the new learning for the second eye.

retained when the target was moved from the first to the second locality (see Fig. 2) or when the trained background was changed. This strong monocularity is in contrast to other stimulus-specific discrimination-learning paradigms where no significant monocularity was found (3, 4) but is consistent with the monocularity recently shown for surrounding texture-dependent texture-contrast perception (15).

Throughout these experiments, performance on the concurrent central fixation task was not significantly different from the performance on this task when carried out alone. This indicated that no significant deviation from fixation occurred. Some learning was noted for this task also, mainly during the first sessions for each observer. However, all stimulus manipulations, including monocular switching, had only minor effects (<10 ms) on the central fixation control task.

DISCUSSION

Our results show that the speed with which observers obtain a workable percept of texture objects from an array of oriented bar elements increases with repeated experience. This substantial improvement represents a genuine long-term change in sensitivity; measurements were made with a forced choice procedure, and there was no significant change in the average response bias (16), which was small for all observers, when initial training sessions were compared to the asymptotic sessions.

We have also shown that learning is local in the sense that it only occurs at visual field localities where targets were repeatedly presented and is not specific for the particular target-element orientation but rather for the background-element orientation. Previously reported orientation-specific form (1, 3)- and motion (4)-discrimination learning was local in a sense that it was not transferrable to unstimulated (blank) visual field localities, and so learning could have been ascribed to repeated stimulus exposure *per se*. Here we show that, although learning is specific for background orientation, repeated exposure to background elements *per se* is not enough to affect texture-discrimination learning because

learning is restricted to the target texture's location. This apparent paradox can be resolved by assuming that learning occurs where texture gradients (relative to a specific background) are available as essential input. Our discovery of background-element orientation specificity implies that learning involves either horizontal connections between units with similar orientation tuning (this type of connectivity has been described in the V1 cortical visual processing area; ref. 17) or gradient-sensitive mechanisms that compute gradients relative to a specific (reference) orientation (figure 4 in ref. 18) or involves both of these mechanisms.

Where does learning occur? Our results suggest that a substantial part of texture discrimination learning is effected at a level within the visual system where the retinotopic organization of the visual input and a high degree of monocularity are still retained and where different orientations are processed separately. In primate visual cortex there are several visual processing areas where retinotopy and orientation selectivity are expressed (10, 11). But our results provide more constraints for loci involved in learning. (i) Learning occurs only at specific sites where orientation gradients are available as essential input so presumably an orientation gradient-sensitive mechanism is involved. Recently, single-unit recordings from macaque monkeys visual cortex using displays quite similar to the one used in the present work has revealed surrounding texture-dependent neurons that respond to texture gradients but not to uniform textures in areas V1 and V2 (18). (ii) The significant monocularity of the effect suggests that learning involves visual processing at or before area 17, where neurons preferentially respond to input from one retina and so are committed to processing information from a specific eye. Orientation-selective monocular cells are found only in V1, the earliest cortical visual processing area in primates (10, 19).

The results of this study strongly support the localization of texture discrimination learning to long-term experience-dependent changes in adult primary visual cortex. If so, this is the first demonstration of a high degree of plasticity within the human primary visual cortex that is relevant to our ability to improve and learn perceptual skills. We suggest that these results can be interpreted in terms of local, retinal input-dependent modifications of the neuronal connections between orientation-selective cells and gradient-sensitive cells in area 17. A strictly reductionist interpretation is possible. The core idea is Hebbian: use-dependent synaptic enhancement induced by concurrent pre- and postsynaptic activity (20). We consider the interaction of two cell types: a first-level cell that is orientation selective and a second-level cell that responds to simultaneous activity in disparate first-level cells from within a specific [quite large (18)] retinotopic neighborhood (surrounding texture dependence). We have shown that learning does not occur at locations of uniform texture (background *per se*) where only first-level units will be activated—i.e., learning does not depend on the local signal level in orientation-selective cells alone. But at locations corresponding to texture borders, a concurrent vigorous activation of both first-level (“presynaptic”) and second-level (“postsynaptic”) cells will occur, leading to enhanced synaptic connections with repeated stimulus presentations. Such an interpretation could provide a possible explanation for the unusual time course of texture-discrimination learning in terms of synaptic “consolidation” between sessions, possibly by a mechanism similar to the progression of input-dependent selectivity commitment of visual neurons several hours after visual experience was terminated (21).

Learning may also involve the improvement of links from local gradient-sensitive mechanisms to global discrimination processing. Hebbian learning could affect the output end of second-level cells and their connection to higher level neurons, provided a concurrent input is available to activate

these higher level cells either from the stimulus or from extraretinal sources (22, 23). A third locus for learning may reside in improved lateral inhibitory connections between highly specific monocular units tuned for background orientation and subserving specific visual-field locations. Then practice could reduce background noise and strengthen the "pop out" of the target. A mechanism of specific lateral inhibition has been suggested for texture-contrast gain control, which was ascribed to an early cortical or precortical neural locus (15) and as a general model of texture discrimination (24). However, such a model does not easily explain why background learning is determined by the target's location.

Though by no means conclusive, these interpretations suggest the possible reduction of a human learning process to local cortical functional plasticity. It remains to be seen how other parameters (e.g., extraretinal input[‡]) affect texture discrimination learning and to what extent the predictions of the perceptual learning–functional plasticity analogy could be generalized to shed light on other sensory and motor learning paradigms.

[‡]The perceptual learning–functional plasticity analogy requires some extraretinal control mechanism to modulate and gate functional plasticity—i.e., control the adaptive state of cortical neurons (22, 23). This probably accounts for the fact that plasticity occurs in adult mammalian cortex only if behaviorally relevant (25). Recent results indicate that texture discrimination learning is indeed affected only if stimulus input (orientation gradients) is task relevant (26).

We thank Drs. Y. Dudai and R. Malach for helpful discussions and acknowledge support by the Israeli Center for Psychobiology.

1. Ramachandran, V. S. & Braddick, O. J. (1973) *Perception* **2**, 371–376.
2. McKee, S. P. & Westheimer, G. (1978) *Percept. Psychophys.* **24**, 258–262.
3. Fiorentini, A. & Berardi, N. (1981) *Vision Res.* **21**, 1149–1158.
4. Ball, K. & Sekuler, R. (1987) *Vision Res.* **27**, 953–965.
5. Beck, J., ed. (1982) *Organization and Representation in Perception* (Erlbaum, Hillsdale, NJ), pp. 285–317.
6. Julesz, B. (1984) in *Dynamic Aspects of Neocortical Function*, eds. Edelman, G. M., Cowan, W. M. & Gall, W. E. (Wiley, New York), pp. 585–612.
7. Marr, D. (1982) *Vision* (Freeman, San Francisco), pp. 49–86.
8. Sagi, D. & Julesz, B. (1985) *Science* **228**, 1217–1219.
9. Gurnsey, R. & Browse, R. A. (1987) *Percept. Psychophys.* **41**, 239–252.
10. Zeki, S. M. (1978) *Nature (London)* **274**, 423–428.
11. Hubel, D. (1982) *Nature (London)* **299**, 515–524.
12. Nothdurft, H. C. (1985) *Vision Res.* **25**, 551–560.
13. Sagi, D. & Julesz, B. (1985) *Spatial Vision* **1**, 141–149.
14. Bergen, J. R. & Julesz, B. (1983) *Nature (London)* **303**, 696–698.
15. Chubb, C., Sperling, G. & Solomon, J. A. (1989) *Proc. Natl. Acad. Sci. USA* **86**, 9631–9635.
16. McFadden, D. (1970) *Percept. Psychophys.* **8**, 336–342.
17. Gilbert, C. D. & Wiesel, T. N. (1989) *J. Neurosci.* **9**, 2432–2442.
18. Van Essen, D. C., DeYoe, E. A., Olavarria, J. F., Knierim, J. J., Fox, J. M., Sagi, D. & Julesz, B. (1989) in *Neural Mechanisms of Visual Perception*, eds. Lam, D. M. K. & Gilbert, C. (Portfolio, Woodlands, TX), pp. 137–154.
19. Livingstone, M. S. & Hubel, D. H. (1984) *J. Neurosci.* **4**, 309–356.
20. Brown, T. H., Chapman, P. F., Kairiss, E. W. & Kearman, C. L. (1988) *Science* **242**, 724–728.
21. Buisseret, P., Gary-Bobo, E. & Imbert, M. (1978) *Nature (London)* **272**, 816–817.
22. Fregnac, Y., Shulz, D., Thorpe, S. & Bienenstock, E. (1988) *Nature (London)* **333**, 367–370.
23. Heggelund, P., Imamura, K. & Kasamatsu, T. (1987) *Exp. Brain Res.* **68**, 593–605.
24. Sagi, D. (1990) *Vision Res.* **30**, 1377–1388.
25. Singer, W., Treter, F. & Yinon, U. (1982) *J. Physiol. (London)* **324**, 239–248.
26. Karni, A. & Sagi, D. (1990) *Invest. Ophthalm. Vis. Sci.* **31**, 562 (abstr.).